XXIV. Of the Developement of the seminal Germ. By the Rev. Patrick Keith, F.L.S.

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Read November 16, 1813.

No phænomenon observable in the process of germination has excited so much wonder, and remained at the same time so totally inexplicable, as that of the invincible tendency of the radicle and plumelet to insinuate themselves respectively into the soil and atmosphere, independent and in despite of all accidental obstacles that may happen to be thrown in their way.

If a seed or nut of any sort is placed in the proper soil with the apex of the radicle pointing downwards, the radicle as it elongates will descend in a perpendicular direction and fix itself in the earth; and the plumelet issuing from the opposite extremity of the seed will assume a vertical direction and ascend into the air. This is the natural order of the developement of the seminal germ; and from the relative situation of its respective parts its developement does not seem to be at all surprising. But the circumstance exciting our surprise is, that the radicle and plumelet will still continue to effect their developement invariably in the same manner, whatever may have been the original position in which the seed was deposited in the soil. For, if its position shall happen to have been accidentally inverted, so as that the radicle shall be uppermost and the plumelet undermost, the former will then bend itself down till it gets a hold of the soil, and

and the latter will in like manner bend itself up till it reaches the air. And no human art has ever been able to make them assume contrary directions, or to convert the one into the other, as the root and branches of the vegetating plant may afterwards be sometimes converted.

Du Hamel, whom no phytologist has ever surpassed in the invention of expedients to unmask or to control the operations of the vegetative principle, instituted a variety of experiments with a view to effect this conversion, and failed in them all. He first placed an acorn between two wet sponges suspended from the ceiling of his room, so as that the radicle was uppermost and the plumelet undermost. The result however was, that the radicle, after bursting its integuments, assumed a downward direction, and the plumelet in its turn an upward direction, till each had gained its natural position. He then filled a tube with earth, and planted also an acorn in it in an inverted position. But the radicle and plumelet had no sooner escaped from their envelopes, than they began to assume their natural direction as before. He then filled another tube with earth, of a diameter so small, that an acorn when introduced into it touched the internal surface on all sides. It was planted in its natural position, and allowed to remain so till the radicle appeared. The tube was then inverted, and the radicle began immediately to bend itself downwards. The tube was again inverted, and the radicle resumed its original direction*. aliens of the state of the stat

Such is the invincible tendency of the radicle to fix itself in the soil, and of the plumelet to escape into the air. How is this tendency to be accounted for? A great many conjectures have been offered in reply to the inquiry, without having done much to elucidate the subject. Some have attributed the phænomenon

^{*} Physique des Arbres, tome ii. chap. 6.

to the excess of the specific gravity of the juices of the radicle beyond that of the juices of the plumelet, which in their progress upwards were supposed to be reduced by the process of elaboration to a light vapour. But this is by no means known to be the fact; or, rather, it is known not to be the fact, and consequently forms no ground of argument. Others have attributed it to the respective action of the sun and earth; the former attracting the leaves and stem, and the latter attracting the root. But it happens rather unfortunately for the conjecture, that the phænomenon is exactly the same even when seeds are made to vegetate in the dark. Du Hamel repeated the experiment in a dark room, and obtained the same result as in the light. The influence of the sun was then transferred to that of the air, which was thought to have some peculiar attraction for the plumelet that the earth had not. But the attraction of the air was just as mysterious as that of the sun, and the subject as much in want of elucidation as before.

In this stage of the inquiry Dr. Darwin, of philosophical and poetical memory, undertook the explication of the phænomenon, and endeavoured to account for it chiefly upon the principle now specified, the radicle being presumed to be stimulated by moisture, and the cotyledons and plumelet by air, and each to be hence elongated in the direction of its exciting cause*, which is precisely the direction assumed by the radicle and plumelet respectively in the actual developement of the seminal germ; the former descending into the earth, as being excited by the action of moisture, and the latter ascending into the atmosphere, as being excited by the action of the air.

This hypothesis is, no doubt, sufficiently ingenious, but is by no means to be regarded as a satisfactory solution of the difficulty. For at this rate all cotyledons, germinating in their natural soil,

[#] Phytolog. sect. ix.

ought to rise above ground in obedience to the stimulus of air, which all cotyledons do not; and all seeds ought to germinate, if not in the water, at least in the earth, though many of them will germinate in neither; but on trunks and stumps of trees, as many of the Mosses; or on the bare and flinty rock, as many of the Lichens. And if the radicle is naturally stimulated by moisture, and the cotyledons and plumelet by air, and each elongated in the direction of its exciter; then, if an inverted seed is so placed by art that moisture shall reach it only from above, and air only from below, the radicle ought unquestionably to elongate itself by ascent, because that is the direction of its exciter; and the plumelet ought also to elongate itself by descent, because that is the direction of its exciter. But this did not happen in the case of any of Du Hamel's inversions, in one or other of which the supposed conditions must have been almost literally fulfilled; nor did it happen in the case of the following experiment, which was instituted expressly for the purpose of putting Dr. Darwin's hypothesis to the test.

On the 24th of July 1812 I procured a tube of glass of four inches in length, and nearly an inch in diameter, which I filled with garden mould, and suspended from the ceiling of my study. Into the lower extremity of the tube I then introduced a kidney-bean and a grain of wheat, inserting them in the mould by somewhat more than the one-half, with the apex of the radicle upwards, and the base of the seed touching the inner surface of the tube, that the process of germination might be readily traced through the glass. The earth was then almost wholly above them; and the water with which it was occasionally moistened was applied at the upper extremity, so as to come to the seeds from above, as well as in small quantities at a time, so as just to wet the mould sufficiently, but not to ooze out at the lower extremity.

tremity. Such were the preparations for experiment. What was the result?

On the 25th of July the bean and grain of wheat were swoln with moisture that had reached them from above, and were apparently in a state of incipient germination.

On the 26th of July, at nine o'clock in the morning, the radicle of the bean, which had burst its integuments, was found to have elongated in a straight and horizontal direction to the extent of about nearly a quarter of an inch. At mid-day its elongation was perceptibly advanced, and the apex was just beginning to assume a bend downwards. At nine o'clock in the evening it was found to have elongated in a descending direction to the extent of nearly half an inch, and was so much bent downwards as to exhibit the figure of a sort of hook or sickle, though there was no earth below it, and no moisture coming to it except from above. The radicle of the grain of wheat had not yet burst its integuments.

On the 27th of July, at nine o'clock in the morning, the radicle of the grain was seen projecting beyond its integuments, and as yet ascending at an angle of 45 degrees, or rather forming a sort of faint bend, being only one-twelfth of an inch in length. At nine o'clock in the evening it measured a quarter of an inch in length, and was bent down at the extremity in a perpendicular direction, accumbent on the inner surface of the tube; but the sheath of the plumelet had not yet burst the envelopes of the seed. The radicle of the bean measured nearly three quarters of an inch in length, having descended in a perpendicular direction, and in the open air, below the extremity both of the earth and tube.

On the 28th of July the radicle of the bean had not advanced much in length, but had augmented considerably in thickness.

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The radicle of the grain measured about half an inch in length, having descended, like that of the bean, till it passed the lower extremity of the tube, though there was no earth in its course, and no moisture coming to it but from above. The sheath of the plumelet had just begun to project beyond the integuments of the seed.

On the 29th of July, at mid-day, the sheath of the plumelet or cotyledon of the grain measured a quarter of an inch in length, having extended in a straight line, sloping a little downwards, with the point ascending, but not more than just perceptibly so. The main fibre of the root measured an inch and a half in length, and the two lateral fibres about an inch each, having assumed now a direction rather horizontal, and along the under surface of the earth of the tube, with the point also ascending. The radicle of the bean had increased much in thickness, and sent out lateral and descending fibres. But the main or tap root had assumed a horizontal direction at the lower extremity, in the manner of the fibres issuing from the grain. At ten o'clock at night the cotyledon of the grain measured nearly half an inch in length, and was evidently bent upwards at the point, forcing its way through the earth, and ascending by the side of the tube, so that its progress was very easily traced.

On the 30th of July the cotyledon of the grain had elongated somewhat in the night, and in the ascending direction it had assumed the day before, being quite half an inch in length. The plumelet of the bean had not yet escaped from within the lobes of the cotyledon, owing, I suppose, to the confined situation in which the seed was placed within the tube, as well as to the want of due nourishment, arising from the circumstance of the root's being now almost wholly below the earth. Indeed the germination both of the bean and grain was much less rapid and vigorous

vigorous than it would otherwise have been at the same season of the year, owing to the tendency by which the radicle and plumelet assumed respectively a descending and ascending direction, thus quitting the sources of nourishment that were placed next to them, in order to reach other sources that were placed at a distance.

On the 31st of July, at nine o'clock in the morning, the cotyledon of the grain was an inch in length, surmounted by the summit of the first real leaf, that projected beyond it by about a quarter of an inch, with an inflected point, and forming, together with the cotyledon, the figure of a hook or sickle. At nine o'clock in the evening, the summit of the first leaf, still inflected at the point, surmounted the sheath by about half an inch. Its elongation was still vertical, and its sickle-like bend lower than even the bottom of the tube, as if forcing itself down into the open air. The bean was also bent down by the stem in the same manner; but the lateral fibres sent out by the radicle were rather ascending into the earth above them. The lobes of the cotyledon were so far separated as to show that the plumelet had ascended vertically within them, and was just about to emerge from between them.

On the 1st of August the shoot of the grain of wheat, which measured an inch and a half in length, and still continued to ascend in a vertical direction through the earth, was in its second leaf; while the plumelet of the bean, which had just begun to protrude its divisions beyond the contour of the cotyledons, was found to have elongated itself wholly in a vertical line.

In the above stage of advancement the experiment was put an end to; it having been already sufficiently proved that Dr. Darwin's hypothesis could not possibly be true, since the radicle was still elongated by descent, even when the earth and moisture

were placed above it; and the plumelet, on the contrary, by ascent, even when the access of air was possible only from below. If the points of the roots or fibres became horizontal or even ascending in the latter part of the experiment, it is to be recollected that germination was then past; and that the extremities of vegetating roots are often found to deviate from the line of descent in quest of a more fertile portion of soil.

But although the insufficiency of Dr. Darwin's hypothesis should even be admitted, there remains yet another hypothesis to combat. For Mr. Knight, whose meritorious labours in Phytology are too well known to this Society to stand in need of any encomium from me, has still more recently attempted to account for the descent of the radicle upon the old but revived principle of gravitation, strengthened, as he no doubt thinks, by the following results of experiment.

Beans, which were made to germinate after being fastened in all positions to an upright and revolving wheel, that performed 150 revolutions in a minute, uniformly directed the radicle outwards from the centre, and the plumelet inwards to the centre: and beans that were so fastened to a horizontal and revolving wheel, performing the same number of revolutions in the same space of time, uniformly protruded their radicles obliquely outwards and downwards, and their plumelets obliquely inwards and upwards*; which effects Mr. Knight regards as resulting from the centrifugal influence of the wheel's motion counteracting that of gravitation, which is consequently, in his opinion, and in the natural position of the seed, the cause of the radicle's descent.

This conclusion, if it has not been adopted by botanists in general, has been adopted at least by Sir Humphry Davy, one of the most illustrious chemists and phytologists of the present

problem that forms the subject of the present Paper*. To arguments, therefore, conflicting with such high authorities, it may well be supposed that I do not solicit the notice of this learned.

and enlightened Society but with fear and trembling.

But the grand defect of Mr. Knight's hypothesis is, that it does not at all account for the ascent of the plumelet, unless my recollection of his Paper on this subject is itself defective. And indeed the ascent of the plumelet upon Mr. Knight's principles. seems to me to be next to impossible, though it is made to ascend. notwithstanding. For if the principle of gravitation is found to act so very powerfully upon the radicle, should it not be found to act also in a similar manner upon the plumelet, and to prevent its ascent altogether? which, if it is not so heavy as the radicle, is at least specifically heavier than atmospheric air, and ought consequently to be subject to the influence of gravitation. We cannot, therefore, regard the power of gravitation as being the cause of the radicle's descent, unless we are at the same time shown how it comes to exert no influence upon the plumelet. Much less are we to regard it in that light, if it can be shown, on the contrary, that there are cases in which the radicle is developed in a direction totally opposite to that of the force of gravitation, that is, by ascent, as may be exemplified in the germination of the seed of the misseltoe.

The seeds of this plant germinate, as is well known, not in the ground, but on branches of the oak or apple-tree; or it may be of some other tree, where they are accidentally left by birds. They will also germinate even when made to adhere to a branch by means of human aid; which, from their glutinous nature, they may readily be made to do, though I have not myself been

^{*} Lectures on Agric. Chem. p. 30.

But according to the account of Du Hamel, the seeds of the misseltoe germinate by sending out a small and globular body attached to a pedicle, which, after it acquires a certain length, (about one-fourth of an inch I believe,) bends ultimately towards the bark, into which it insinuates itself by means of a number of small fibres, which it now protrudes, and by which it abstracts from the supporting plant the nourishment necessary to its future developement. When the root has thus fixed itself in the bark, the stem of the parasite begins to ascend, at first simple and tapering, and of a pale green colour, but finally protruding a multiplicity of branches by continually dividing into jointed forks.

Hamel I adopt it as the fact, it will be easy to show that the elongation of the radicle of the seed in question must necessarily be by ascent, because it is also a fact that almost all plants of the misseltoe originate in the lower surface of the bough on which they grow. Whatever, therefore, may have been the original direction of the radicle, its ultimate direction must be that of ascent, before it can possibly reach the bark into which it is to fix itself. Now this is a case directly counter to the assumed principle of gravitation, which, till it is satisfactorily accounted for, cannot but be regarded as presenting an insuperable obstacle to the adoption of Mr. Knight's hypothesis.

There is, however, a view of the subject which I have sometimes regarded as giving even to the hypothesis of Mr. Knight a degree of plausibility worthy of some consideration. It appears from the experiments of Du Hamel, which seem to have been repeated by Mr. Knight, that the radicle and plumelet do not augment their mass in the same manner. The former elongates chiefly by the apex, while the latter elongates by means of the

intro-susception of particles deposited throughout the whole of its extent. If, therefore, we regard the additions deposited at the point of the radicle, as being originally almost fluid, which they must indeed be, we shall then find in that fluidity a cause apparently adequate to the effect; the part deposited being thus immediately subject to the law of gravitation, and incapable of supporting itself in a vertical position, even though placed in the soil. And in like manner the mode of augmentation displayed by the plumelet or stem seems calculated rather to facilitate the ascending direction, which it actually assumes from the support that is thus gradually distributed throughout the whole of its extent. And hence a sort of plausibility is given to the hypothesis.

But after all it will not bear the test of a rigid scrutiny; for it will not account for the ascent of the radicle in the case of the misseltoe, because the force of gravitation is here counteracted; nor for the re-assumption of a vertical position by the plumelet that has been inverted, because its mode of growth seems favourable to elongation only in a straight line; nor for the phenomenon of the pendent stem, as in the case of Cactus flabelliformis and others; because, upon the very principle assumed, its growth ought to have been upright.

The radicle does not therefore descend by virtue of the law of gravitation, nor of the attraction of moisture: but by virtue of an energy exerted in the direction of gravitation, and guiding it infallibly to nourishment and support; and the plumelet does not ascend by virtue of the principle of levity, or of the attraction of the air, but by virtue of an energy exerted in opposition to that of gravitation, and leading it infallibly to the atmosphere above it; so that even in cases of unnatural and inverted experiment the energy still acts, and the radicle and plumelet elongate according to the law originally imposed upon them, though it be

even to the prejudice of their own augmentation, by withdrawing them respectively from the sources of nourishment that are immediately contiguous to them, in order to reach sources that are more distant. But when nature has intended a different mode of developement, as in the case of the seeds of the misseltoe, it has also been able to command it, and to give even to the radicle the power of counteracting the force of gravitation, and of elongating by means of ascent.

What, then, is this controuling and invincible energy that presides over the process of germination, guiding the radicle infallibly to its fit and proper soil, whether in the earth or otherwise, as well as elevating the plumelet till it escapes into the air or other proper medium of developement? Is it not an attribute of the vital principle of the plant itself, impelling it irresistibly, though blindly, to the attainment of an end? The case seems loudly to demand the agency of such a cause, and points out plainly the exertion of an energy that cannot be regarded as being either merely chemical or mechanical.

Perhaps we may be able to elicit some rays of information from a reference to the economy of the animal kingdom in cases that are analogous. For if you ask the Zoologist why it is that the foal of an ass, from the moment it is protruded into life, never fails to discover the source from which its nourishment is to be derived, nor the organ proper for laying hold of it: the reply will be, that it is because the Creator has wisely endowed it with a principle of action impelling it to the use of the natural means of self-preservation, and operating infallibly to the attainment of an end, without any thing of intention on the part of the agent.

But if this principle, which has been denominated animal instinct, is admitted in the animal kingdom, why may not a similar principle, to be denominated vegetable instinct, be admitted

in the vegetable kingdom? The necessity is in both cases the same; the support and preservation of life, of which the vegetable exhibits indubitable indications as well as the animal, though inferior in degree. And the principle has indeed been claimed, particularly, as I believe, by Dr. Percival of Manchester, though I am not acquainted with the grounds on which he rests his claim, not having hitherto had an opportunity of consulting his Paper on the subject. But on whatever grounds the claim may have been advanced, it cannot by any means be regarded as extravagant or absurd, sanctioned as it is by the analogy of the animal kingdom, and by the necessity of assigning a cause adequate to the production of the effect. For if we must acknowledge that no cause merely chemical or mechanical is sufficient to account for the direction that is invincibly assumed by the radicle and plumelet respectively, in the process of the germination of the seed, we must also of necessity admit the agency of some cause of a higher order, which can be nothing short of an attribute of the vital principle of the plant itself. And the lowest cause we can possibly assign, as well as the only cause we can warrantably assign, is that of an attribute that shall be analogous to the faculty of animal instinct, as being the lowest principle of action influencing a living being; and the only acknowledged cause found to operate in analogous cases; as well as perhaps the only efficient cause by which the apparently spontaneous movements of the plant are in any case directed.

Some of the ancients seem indeed to have claimed for plants principles of action of a much higher order, and to have attributed the desires and passions of animals even to the vegetable race*, thus regarding as a fact, what the author of The Loves of Plants regarded no doubt as a fiction, and elevating the vegetable

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almost to the rank of the animal. But this is evidently an extravagant assumption, which the phenomena of vegetable life will by no means warrant, and which cannot consequently be admitted. Others, more moderate in their assumptions, have been contented with claiming for vegetables the faculty of sensation, alleging that there are phenomena exhibited within the extent of the vegetable kingdom, which it is impossible to account for on any other principle; such as that of the irritability of the sensitive plant, the fecundation of the valisneria, the sleep of the papilionaceæ, and others. But whatever may be the value or fate of this claim, it does not at all affect the merits of the claim now advanced. For, in the first place, it does not necessarily involve the attribute either of animal passion or sensation, any more than it involves the faculty either of seeing or hearing; as being altogether the instinct of a different order of being. In the second place, it is sufficiently elevated above any cause merely chemical or mechanical, to sanction the belief of its adequacy to the production of the effect ascribed to it. And, in the third place, it is claimed. only in a case analogous to that in which a similar principle is acknowledged to act in the animal subject. Whence we infer the agency of an instinctive principle in the vegetable subject also, as being the key that opens up the way to the solution of the difficulty in question, and unriddles the mystery of the developement of the seminal Germ, without which it is indeed altogether incomprehensible; but with which it admits of an easy and luminous explication, drawing closer the analogy that subsists between the animal and vegetable kingdoms, and enhancing our notions of the wisdom of the Divine Mind.

Thus, then, it is that the attribute of vegetable instinct, acting agreeably to the original impulse communicated to it by the hand of nature, directs the radicle uniformly downwards, and in con-

currence with the agency of gravitation, when the proper conditions of germination are present, regardless of all obstacles or inducements tending to divert it from its course, as being the natural direction of its proper aliment and support, except in such cases as are exemplified in the germination of the misseltoe; while it directs the plumelet uniformly upwards, and in opposition to the agency of gravitation, when the above proper conditions are present, as being the natural direction of the medium that is the best suited to the developement of its parts.

If it is said that the attribute of vegetable instinct is still but an occult quality of an occult principle, of the abstract nature of which we know nothing, the objections we confess must be admitted; but the case is without remedy, as it is in the animal kingdom also, in which we know nothing of the nature even of the human mind itself, except from its operations.

We do not, however, affect to exalt the living principle of the plant to the dignified rank either of a dryad or a sylph, the notion of whose fabled agency has been represented by Sir Humphry Davy as being equally credible with that of the philosopher who shall assume the agency of "any thing beyond common matter, any thing immaterial in the vegetable œconomy*." And yet the agency of some such principle is so absolutely indispensable, that even while it is thus almost directly denied, it seems to me to be indirectly admitted; unless I have altogether misapprehended the concessions which Sir Humphry makes on this subject. For although he thinks there are few philosophers who would be inclined to assert the agency of any thing beyond common matter in the vegetable œconomy, yet he admits that vegetables may be truly said to be living systems, in as much as they possess the means of converting the elements of common matter

into organized structures*. Now, what are we to understand by the means here alluded to, which are evidently an admission of something more than merely common matter? We are not indeed informed in direct terms, but we are warranted in inferring, that the means here alluded to are neither more nor less than life itself; which is represented as rendering the analysis of the vegetable subject exceedingly complicated in comparison with that of inorganic bodies, "by its giving a peculiar character to all its productions, the power of attraction and repulsion, combination and decomposition, being subservient to it †." If, therefore, Sir Humphry Davy is not an advocate for the doctrine of materialism, and life merely an attribute of organization, and matter capable of organizing itself, which is absurd, he admits all we contend for, namely, the existence and agency of a living principle, in the common acceptation of the term, on which the functions of the vegetable organs depend, and in which we maintain that a species of instinct may certainly reside, similar in kind to that of animal instinct, but inferior in degree, as being the guide and director of an inferior nature, conspiring to promote the ends of vegetable life, and acting with unconscious but unerring aim.

But still there remains a circumstance unexplained, that is at least closely connected with the present subject, namely, the impossibility of converting the radicle into the plumelet, or the plumelet into the radicle, as the root and branches of the vegetating plant may afterwards be sometimes converted. For if the stem of a young plum- or cherry-tree, but particularly of a willow, is taken in the autumn, and bent so as that one-half of the top may be laid in the earth, one half of the root being at the

^{*} Agricultural Chem. Lect. v. † Elem. of Agricultural Chem. Lect. ii. vol. xI. 2 N same

same time taken carefully up and gradually exposed to the cold, and the remaining part of the top and root subjected to the same process in the following year, the branches of the top will become roots, and the ramifications of the root will become branches, protruding leaves, flowers, and fruit in due season*.

How then is the anomaly of the successful inversion of the vegetating plant to be accounted for, since no art has yet been able to effect it in the seminal germ? This is a difficulty for which I do not recollect to have seen any solution offered; and in the want of all other plausible conjecture I submit the following: The embryo of the seed is an individual and solitary germ, whose developement is necessarily effected in a determinate manner, owing to the peculiar structure and organization of its parts, and peculiar action of the instinctive principle; that is, by the descent of the radicle into the earth, and ascent of the plumelet into the air, or into the soil and medium respectively suited to each. It could not, therefore, succeed by being inverted, because the radicle and plumelet contain as yet no principle whose developement could be effected in any other way; so that you might just as well expect a child to walk upon its hands, as a seed to germinate by the descent of the plumelet.

But the case is not the same with the vegetating and inverted plant. Its roots and branches contain now multitudes of buds or germs which have been acquired in the process of vegetation, and which, according to the doctrine of Du Hamel, I shall suppose to be plants in miniature, containing the rudiments of every thing necessary to the perfection of the species. Consequently they contain a part equivalent to the radicle of the embryo, and capable of being converted into a root, when placed in a proper

soil, as well as a part equivalent to the plumelet, and capable also of being converted into a branch when placed in a proper medium. But the earth affords the proper soil to the one, and the air the proper medium to the other, the powers of vegetation are again exerted, and the inverted plant grows.

If it is said that the existence of the germs in question is merely a gratuitous assumption without proof, I shall only beg to add, that I do not positively insist upon the reality of their existence; but contend that if they should prove to be a non-entity, still the power of inverted vegetation must be admitted to be a power acquired in the process of the plant's growth, dependent upon the principle of propagation by slips and layers, and consequently not possessed by the seminal germ; in the same manner that the power of producing its kind is not possessed by the animal at the time of its birth, but acquired at an after period.

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